

Initial Responses of Dung Beetle Communities to Bison Reintroduction in Restored and Remnant Tallgrass Prairie

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ABSTRACT

Restoration is a critical component of grassland conservation worldwide, but grassland management requires disturbances that maintain the habitat. Further, successful restorations need to support not just a vegetative community, but also a diverse community of other organisms that contribute to a range of ecosystem functions. Large herbivore grazers like American bison (*Bison bison*) can be an important part of these management strategies, but their role in functions like nutrient cycling relies in part on dung beetles (Scarabaeidae: Scarabaeinae and Aphodiinae, and Geotrupidae), which provide valuable ecosystem services by removing and burying dung. We evaluated dung beetle community responses and dung decomposition in restored and remnant prairies shortly (1.5 y) after bison reintroduction. Dung beetle abundance was significantly greater where bison were present, where prescribed fire had been applied in the past year, and in older restorations and remnants. These same environmental characteristics also shifted the composition of beetle communities, but not total community biomass, as the increased abundance was driven by small-bodied species. Dung decomposition varied with bison presence and site age, with the highest rates of decomposition in an old restoration with bison present. These results indicate that dung beetle communities are capable of rapidly responding to bison introduction, a promising sign that land managers may be able to reestablish ecosystem-level processes driven by large grazers in restored grasslands.

Index terms: ecosystem restoration; ecosystem service; grazer; prescribed fire; Scarabaeidae; tallgrass prairie

INTRODUCTION

Restoration and conservation of grasslands has taken on prominence worldwide because these are among the most endangered habitats, primarily due to agricultural conversion (Gibson 2009). Managing restored and remnant grasslands usually requires the establishment of disturbance regimes to limit woody plant encroachment, invasions by nonnative plant species, or biodiversity loss due to native dominant competitors (Packard and Mutel 2005). The introduction of large ungulate grazers such as bison (*Bison bison* L.) as a management tool to achieve these goals has occurred or is being considered in tallgrass prairie restorations across the US Midwest (Brockman 2007; Freese et al. 2007; Sanderson et al. 2008; Fox et al. 2012; Allred et al. 2013). Prairie restoration goals are often focused on maintaining or increasing native plant diversity. This mirrors restoration ecology in general where restoration efforts and evaluation of their efficacy are usually focused on reestablishing plant communities, with less attention paid to consumers, detritivores, and the critical ecosystem functions to which they contribute (Hobbs and Norton 1996; Van Andel and Aronson 2012; McAlpine et al. 2016).

Bison may affect other organisms and ecosystem functions as well, although there is considerably less research on this. In addition to removing plant biomass and altering vegetation structure, bison alter soil conditions through trampling, wallowing, and depositing dung and urine (Knapp et al. 1999; McMillan et al. 2010). Feeding and other activities drive fundamental ecosystem functions such as nutrient cycling

(Frank and Evans 1997; Singer and Schoenecker 2003), but these functions involve and rely on additional community members. Manure has high nutrient content, but ensuring the availability of those nutrients for plants and soil-dwelling organisms requires dung decomposers. Dung beetles (Scarabaeidae: Scarabaeinae and Aphodiinae, and Geotrupidae) exemplify this role because they feed on, distribute, and bury solid animal waste. In cattle pastures, dung burying can increase soil nitrogen and significantly reduce nitrogen lost to the atmosphere through volatilization (Bertone et al. 2006; Yamada et al. 2007). There is also evidence that the burying behaviors of dung beetles may aid carbon sequestration (Nichols et al. 2009; Menéndez et al. 2016), which could mitigate greenhouse gas contributions by large herds of grazing ungulates. Dung removal and burying activities influence other functions and processes, contributing to seed dispersal, soil turbation, and increased water infiltration (Nichols et al. 2008; Brown et al. 2010). Thus, dung beetle communities are expected to facilitate functions driven by bison while enhancing additional services.

The impacts of bison on communities and ecosystems also may vary with fire patterns on a landscape. Prescribed fire is a common tool in grasslands to mimic the fires historically lit by lightning strikes and indigenous peoples (Fuhlendorf and Engle 2004; Packard and Mutel 2005). Grazers preferentially feed in recently burned areas where nutritious new plant growth is readily available (Coppedge and Shaw 1998; Fuhlendorf and Engle 2004; Fuhlendorf et al. 2009), and their presence in these

areas may be expected to increase dung beetle populations by providing additional food sources (Verdú et al. 2007; Nichols et al. 2009). Dung removal rates have been positively correlated with dung beetle abundance, biomass, or diversity in previous studies (Klein 1989; Horgan 2005; Lee et al. 2009; Slade et al. 2011), so variation in dung beetle community structure due to the interaction of bison and fire also is expected to result in differences in dung removal services.

Restored prairie plant communities also change in diversity and composition in the years following restoration activities. Frequently, plant species richness and diversity decline as competitively dominant species, especially warm-season C_4 grasses, spread and displace poor competitors (Sluis 2002; Camill et al. 2004; McLachlan and Knispel 2005; Hansen and Gibson 2014; Barber et al. 2017b). The regular prescribed fires that most tallgrass prairie restorations receive may accelerate this process as grasses spread and plant spatial heterogeneity declines (Collins 1992). However, whether dung beetle communities and services shift with these age-related plant community changes, or if the increased resources and heterogeneity caused by bison alter such a pattern, is unknown.

In late 2014, The Nature Conservancy reintroduced bison to Nachusa Grasslands, a 1500 ha preserve in northern Illinois that includes extensive remnant and restored tallgrass prairie. We evaluated the initial impacts of this reintroduction on dung beetle communities and on their ecosystem service, dung decomposition, 1.5 y after the reintroduction. While plant effects of bison activities might be expected to take longer to materialize in these perennial-dominated communities, immediately adding the resources that result from the conversion of plant biomass to dung is expected to change the abundance and composition of dung beetle communities. We predicted that dung beetle abundance and diversity would increase with grazer presence and that this effect would be amplified by prescribed fire as grazers spent more time in recently burned areas. We also expected dung removal rates to correlate positively with total dung beetle community biomass.

METHODS

Study Site

Nachusa Grasslands is owned and operated by The Nature Conservancy in Lee and Ogle counties, Illinois, USA. Nachusa largely consists of restored and remnant tallgrass prairie, with smaller areas of oak savannah and wetland habitats interspersed. Most prairie at the site is restored from row crop agriculture (generally corn/soy rotation) and is planted with a diverse mix of native forbs and grasses (see Hansen and Gibson [2014] for more details). Prescribed fire is regularly applied in early spring, or occasionally late fall, with most sites burned approximately every 2 y. Bison were reintroduced to the site in October 2014 and had access to all grazer-present sites in this study starting January 2015 and through the full duration of this study. At the start of the study in spring 2015, there were 68 bison in the 600 contiguous and connected hectares to which bison had access (0.14 bison/ha), and 17 calves were born during the course of the study. Other herbivorous mammals, such as white-tailed deer (*Odocoileus virginianus* Zimmerman), Eastern cottontail rabbits

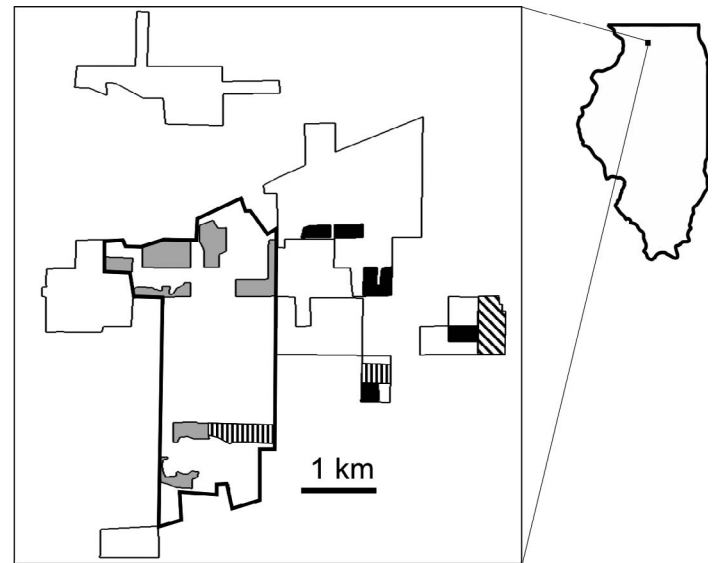


Figure 1.—Map of the study site, Nachusa Grasslands, and location in northern Illinois. Outline is Nachusa property boundaries, and thick line indicates the fenced bison unit. Restorations with bison present are shaded gray, restorations without bison are black, remnants have vertical lines, and the agricultural field has diagonal lines.

(*Sylvilagus floridanus* J.A. Allen), thirteen-lined ground squirrels (*Ictidomys tridecemlineatus* Mitchell), and voles (*Microtus* spp.), are present throughout Nachusa both inside and outside the bison unit.

We selected 12 restored prairies, 2 remnant sites that were grazed but never plowed, and an agricultural field planted in corn to represent pre-restoration conditions (Figure 1). An additional restoration site was included, but an adjacent landowner began grazing sheep near the trapping site, so we excluded this site from analyses. Restorations ranged from 3 to 29 y since planting, and all sites ranged from 5.6 to 20.6 ha in area. Nachusa exists within an agricultural matrix, and most sites are adjacent to both rowcrops (corn or soybean) and other restored or remnant prairie. Seven of the restored prairies and one of the remnants are located within the 600 ha bison unit, which is enclosed by a fence. Bison can move freely among sites within this area, and they are absent from all other sites. One remnant and nine of the restorations were burned in the spring preceding the study (Table 1). Although sampling additional remnants would have been desirable, the rarity of this habitat means that there are no other comparable large remnants within 50 km. Large remnants elsewhere in the Midwest have edaphic, climatic, and historical differences that make them inappropriate references. See Barber et al. (2017c) for more details on the sites used in this study. This design allows us to test bison and fire interactions in a realistic way: prescribed fire is applied to different sites each year based on managers' goals, creating a patchwork of burned and unburned sites at a landscape scale. Bison can choose among these sites for foraging and other activities, within the larger bison unit. But they are excluded from sites outside the bison unit, which are managed with fire in the same way.

Table 1.—Sites used for pitfall trap sampling. Fire indicates whether prescribed fire was applied in the fall or spring preceding the study season.

Site	Year planted	Fire	Bison	Age
HF	2013	Y	Y	3
HN	2012	Y	Y	4
L	2011	Y	Y	5
SB	2009	Y	N	7
CCW	2008	N	N	8
HW	2008	N	Y	8
CCE	2007	Y	N	9
FC	2006	Y	N	10
TC	2002	Y	N	14
SF	2001	Y	N	15
HLP	2001	Y	Y	15
WH	1992	Y	Y	24
MU	1987	N	Y	29
TCR	Remnant	Y	N	—
MR	Remnant	N	Y	—

Community Sampling

We sampled dung beetles in May/June, June/July, and September 2016. In each trapping session (30 May–6 June, 28 June–5 July, and 14–21 September), two pitfall traps (475 mL volume, 8 cm opening) were baited with approximately 10 g fresh bison dung and opened for 7 d. In the September session, three sites were temporarily inaccessible, so these traps remained open for 14 d. However, by the end of each 7 d trapping session, the dung baits were dried out, and capture rates dropped off, so this longer time period was unlikely to inflate captures at these sites. Specimens were identified to species in the laboratory and used to calculate abundance and species richness at each site. Mean individual dry mass for each species was determined from a sample of at least 30 specimens that were dried at 60 °C and was multiplied by species abundances to determine total dung beetle biomass at each site.

Abundance and biomass were summed across all trapping sessions, and species richness was pooled across all sessions to characterize the entire dung beetle community at each site. We analyzed these three variables using generalized linear models with bison presence, prescribed fire, restoration age, and their two-way interactions as fixed factors. Bison presence and prescribed fire (occurred within the last year or not) were categorical variables, and age was a continuous variable. Abundance and richness were analyzed with Poisson error distributions because they are count data, but abundance models used quasi-Poisson distribution because the residual deviance was more than twice the degrees of freedom. Remnants were assigned an age of 32 y, the time since grazing ceased. Because the agricultural field is a radically different habitat (i.e., no fire or possibility of grazing and no “age”), it was not included in these models but is plotted in figures for comparison and to demonstrate that dung beetles are largely absent from sites before restoration takes place. Each interaction and independent variable was evaluated using likelihood ratio tests. Variance inflation factors for age, fire, and bison were all <1.3.

We then examined the effects of bison, fire, and age on community composition with PERMANOVA on Bray-Curtis distances calculated from species abundances standardized by trap-days, with 100,000 permutations, using `adonis()` in the

vegan package (Oksanen et al. 2013). For PERMANOVA, agricultural field was assigned age 0, and remnants were age 32. All analyses were carried out in R 3.4 (R Development Core Team, Vienna, Austria).

Dung Decomposition Experiment

We placed experimental dung pats in a subset of our study sites and recorded mass lost to determine if bison presence or other factors influenced removal rates and if removal was correlated with the dung beetle community. We chose six sites: the two remnants, two old (15 y since planting) restorations, and two young (5 and 7 y since planting) restorations. One site in each age category had bison present. In each site, we weighed and placed 10 dung pats at 10 randomly chosen locations on a 20 m × 40 m grid on 21 and 23 June 2016. Each pat consisted of approximately 80 mL of fresh bison dung that we collected at Nachusa. Fresh mass of experimental dung pats was 88 ± 0.7 g (mean \pm 1 SE, $n = 60$). All dung was frozen to eliminate any arthropods already inhabiting it (Manning et al. 2016) and homogenized after thawing. We visited each site weekly over the next 5 wk to reweigh each pat. The experiment was repeated at the same sites in fall, starting on 20 September 2016 with two changes. First, pats were placed every 5 m along a 45 m transect to assist in relocating them in the tall vegetation. Second, half ($n = 5$ per site, 30 total) of the pats were contained within fine mesh cages that excluded arthropods but allow mass loss due to weathering and microbes to occur. These caged pats allowed us to verify that arthropods were contributing to decomposition.

We analyzed mass loss data with generalized linear mixed models to account for the repeated measures nature of the data and multiple dung pats within each site. Bison presence, site age (young, old, remnant), days since deployment, and their two-way interactions, as well as season (June, September) were fixed factors. Dung pile was a random factor because each pile was measured at multiple time points, nested within site. We evaluated bison presence, age, and their interactions with each other and with days using likelihood ratio tests. Days since deployment and season were retained in the model because they were structural characteristics of the study. Fire was not considered in these models because all but one of the six sites were burned in the previous spring. To verify that insects contributed to dung loss, we compared final proportion mass lost from caged and uncaged pats with site as a random factor.

To determine if dung mass loss was related to dung beetle community characteristics, we used generalized linear mixed models to model proportion dung lost as a function of either total beetle abundance or total beetle biomass, with days since deployment and season as fixed factors. Dung beetle community characteristics were evaluated with likelihood ratio tests.

RESULTS

We captured 707 beetles of 5 species, and dung beetles were present in every study site. A small number of individuals ($n = 10$) were in the genus *Aphodius*, and these were not identified to species. Beetle abundance was 70% greater in bison sites compared to non-bison sites, and there was a significant interaction between prescribed fire and age such that abundance

Table 2.—Results of generalized linear mixed models analyzing activity density, total biomass, and species richness of dung beetles. Test statistic is likelihood ratio (LR) of nested model containing or not containing the variable or interaction of interest. Dashes indicate main effects not tested because they are present in a significant interaction.

	Activity density		Total biomass		Richness	
	LR	P	LR	P	LR	P
Fire	—	—	0.14	0.304	0.04	0.848
Bison	35.45	<0.001	0.10	0.391	0.20	0.654
Age	—	—	0.00	0.995	0.04	0.836
Fire * Bison	0.41	0.690	0.10	0.410	0.04	0.847
Age * Fire	15.63	0.013	0.34	0.109	0.48	0.490
Age * Bison	5.45	0.110	0.08	0.435	0.09	0.769

increased with age but the trend was stronger for unburned sites because of low abundances in young unburned restorations (Table 2, Figure 2). However, we caution overinterpretation of this pattern because the number of unburned sites during our study year was limited. Neither total biomass nor species richness were affected by age, bison, or fire or their interactions. However, PERMANOVA showed that community composition significantly varied with all three variables (Table 3). The compositional differences were greatest between bison and nonbison sites, and we depict these with NMDS (Figure 3).

Dung decomposition was unaffected by the interaction between days since deployment and either bison (LR = 0.03, $P = 0.858$) or age (LR = 2.87, $P = 0.238$). However, the bison*age interaction was significant (LR = 10.47, $P = 0.005$), indicating that bison impacts on decomposition differed with prairie age. Decomposition was greater in bison than non-bison sites for the old restorations but very similar between the two remnants (Figure 4). Proportion mass lost from uncaged pats was 14.1% greater than caged pats (LR = 19.1, $P < 0.001$). Dung decomposition increased with dung beetle abundance, but the

Table 3.—Results of PERMANOVA analyzing dung beetle community composition.

	SS	MS	df	Pseudo-F	P
Age	0.19	0.19	1	3.12	0.027
Fire	0.24	0.24	1	3.92	0.010
Bison	0.40	0.40	1	6.42	<0.001
Residual	0.62	0.06	10		

effect was marginally significant (LR = 3.26, $P = 0.071$). This pattern translated to approximately a 3% increase in decomposition for every 10 additional beetles captured. Decomposition was not related to biomass (LR = 0.11, $P = 0.738$).

DISCUSSION

Successful ecosystem restoration requires the reestablishment of ecosystem functions and the organisms that carry them out. In grasslands, large grazers and fire can be important agents of disturbance that drive functions in conjunction with associated organisms (Hobbs 1996; Fuhlendorf and Engle 2004). We show that reintroduction of bison to restored and remnant tallgrass prairie quickly affected dung beetle communities, such that sites in which bison were present had overall greater abundance and different species composition relative to sites without bison. These bison effects occur against a backdrop of other factors, including the age and prescribed fire status of a site. One of the critical functions these insects provide, dung decomposition, may have been greater in restorations with bison due to these higher beetle abundances, but this pattern is not clear. These findings support the idea that tallgrass prairie restoration and ongoing management supports coprophagous beetle communities, which are capable of a rapid response to bison reintroduction.

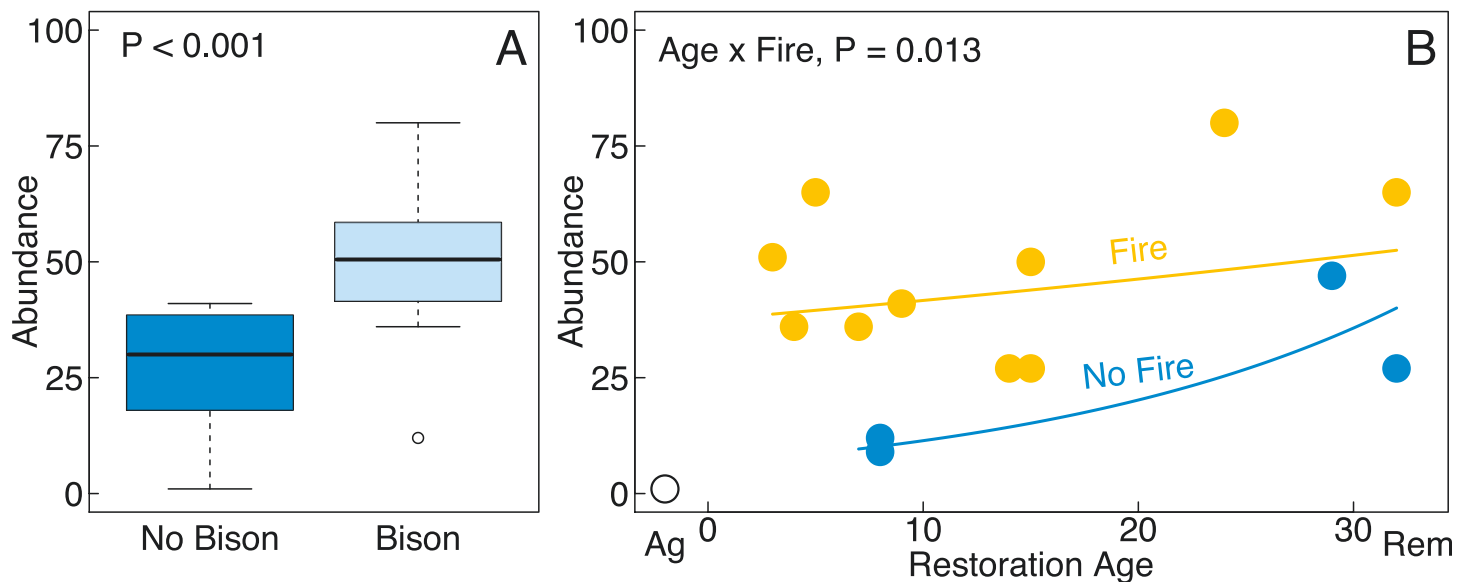


Figure 2.—Abundance of dung beetles by (A) bison presence and by (B) site age and prescribed fire. In (B), open circle “Ag” is agricultural field for reference, and “Rem” is the two remnant prairie sites. Abundance was analyzed with log link function but is plotted on the scale of measurement for interpretability.

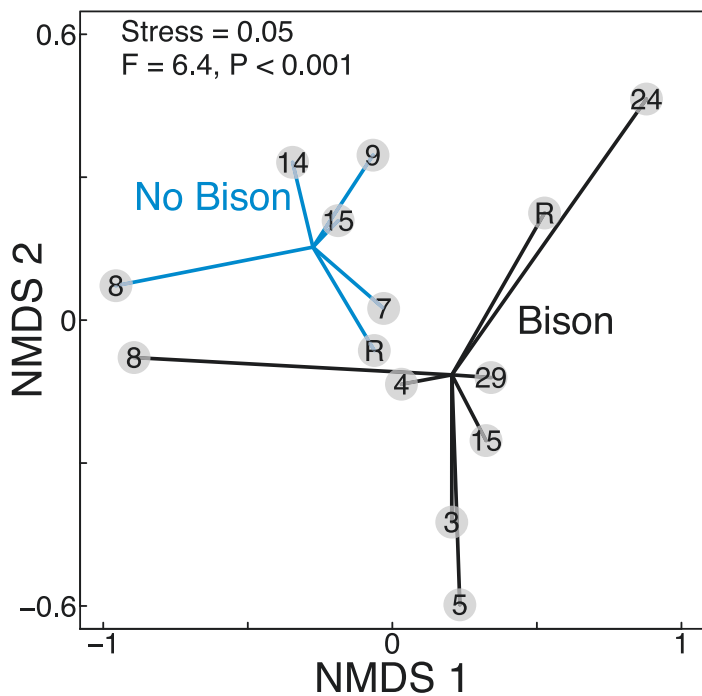


Figure 3.—NMDS ordination of dung beetle community compositions. Sites connected by spiderplot lines have same bison presence or absence. Numbers on each point are ages of that restoration, with “R” indicating remnants. F -statistic indicates comparison of bison presence from PERMANOVA.

Abundance of dung beetles increased with all three management characteristics that we examined: bison presence, restoration age, and prescribed fire application. The direct provisioning of dung resources is a likely explanation for the positive effect of bison. Some other studies actually have found reduced abundance or diversity of dung beetles when comparing grazed sites to adjacent ungrazed habitats (Negro et al. 2011; Audino et

al. 2014). However, these studies examined pastures that were intensively grazed with domesticated herbivores. At such high herbivore densities, negative impacts can even be due to trampling of insects by the grazers (van Klink et al. 2015). In contrast to most domestic cattle ranches, bison stocking density at Nachusa is quite low (0.14 bison/ha or 0.6 bison/acre, counting new calves, in 2016 [E. Bach, pers. comm.]). Prescribed fire also seemed to increase dung beetle abundance, although we present this result with caution because of the limited number of unburned sites in 2016. Prescribed fire is intended to limit woody plants and fire-intolerant herbs, but it also alters habitat structure by eliminating both standing and ground litter from previous years’ growth (Knapp and Seastedt 1986). This could have an effect of increasing beetle mobility to help them locate dung (Hartley et al. 2007; Tocco et al. 2013): a recent study of more arid prairie in Texas found that reduced vegetation density increased dung beetle captures, although reduction of vegetation by fire was not sufficient to cause significant differences in abundance between burned and unburned sites in that system (Smith et al. 2019). If reduced vegetation density or obstruction does make a site more suitable for dung beetles, it could be another potential mechanism for the positive effects of bison that we document because concentrated bison grazing can reduce vegetation height in patches where foraging is concentrated (Coppedge et al. 1998).

Although we predicted that fire and bison presence would interact to amplify effects on dung beetles because bison preferentially feed in recently burned patches (Coppedge and Shaw 1998), we did not detect this effect of pyric herbivory (Fuhlendorf et al. 2009). The pyric herbivory model is scale-dependent and assumes heterogeneous fire causing relatively small burned patches across a landscape. Bison concentrate in these small patches, which also concentrates both grazing impacts on plants and dung deposition (Fuhlendorf and Engle 2001, 2004; Fuhlendorf et al. 2009). Prescribed fires at our study site occur at a larger, management-unit scale comparable to each

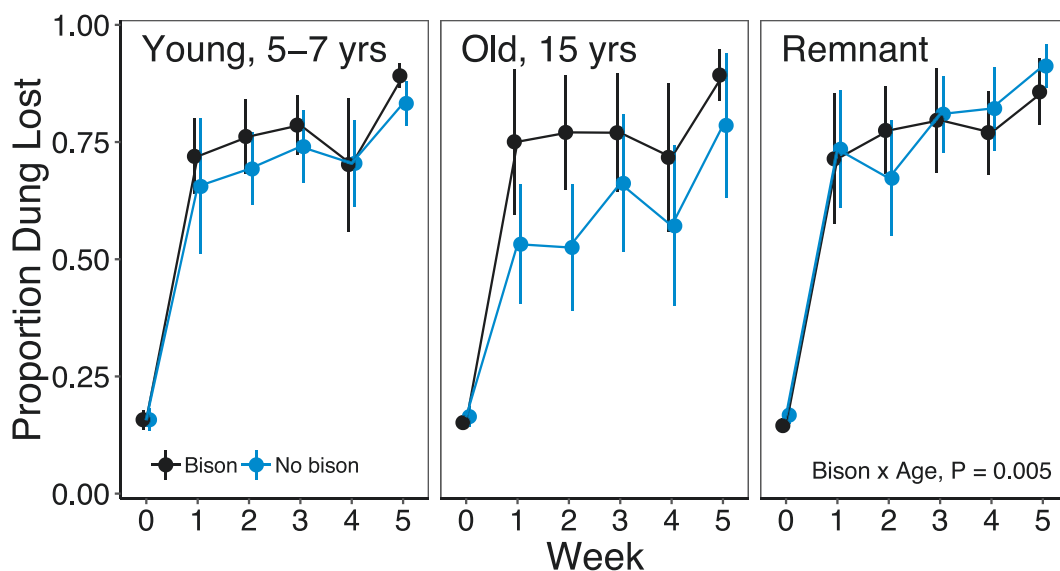


Figure 4.—Proportion mass lost from experimental dung pats by week in each of six restored or remnant prairies, comparing prairies with and without bison. Values are mean proportion lost \pm 1 SD.

of our sites. The bison are very mobile and move across the landscape regularly throughout each day (C. Nielsen, unpub. data), so their impacts are likely to be more diffuse over a larger spatial scale rather than concentrated in small patches. This also means that they may not necessarily be depositing dung directly into the patch from which that plant material originated. If this is the case, these reintroduced grazers may support dung beetle communities more evenly across all sites to which they have access but with a weaker effect than if prescribed fire and the resulting grazing concentration occurred in smaller patches (Allred et al. 2011).

There was a weak increase in dung beetle abundance with site age, but the time necessary after restoration for the beetle community to fully “recover” is unknown. Although abundances in older restorations here were comparable to remnants, these remnants may not be ideal reference sites because their edaphic differences in comparison to restored agricultural fields, with shallower rocky soils on slopes, are the reason they were not converted into farmland. While dung beetle community recovery in other habitats such as tropical forests may occur in two to three decades (Slade et al. 2011) or sooner (Quintero and Roslin 2005), identifying an end-point here may not be possible because there are no existing equivalent remnants (i.e., there are no remnants that are not on shallow-soil slopes) and no detailed historical information. Nonetheless increased abundance with time suggests that certain species are benefiting from the successional changes (Hansen and Gibson 2014; Barber et al. 2017b) that accompany ongoing active management in prairie plantings. Dung beetle species richness did not vary with site age, which contrasts with some other prairie organismal groups. The successional changes in restored prairie plant communities, in which plant richness tends to decline (Sluis 2002; Carter and Blair 2012; Grman et al. 2013; Hansen and Gibson 2014), is accompanied by other richness or diversity declines in ground beetles (Coleoptera: Carabidae; Barber et al. 2017c) and soil microbes (Barber et al. 2017a). But bees, which, like dung beetles, are highly mobile, achieve stable abundance and richness levels within just 2 or 3 y post-restoration (Griffin et al. 2017).

Community composition also changed in response to these environmental factors, particularly bison presence, but richness and total dung beetle biomass did not. This suggests that species respond individually to bison, and to a lesser extent site age and fire application, and increases in one species might compensate for declines in another. In particular, large-bodied species might have declined in abundance following fire or bison disturbances, as susceptibility to disturbance has been documented in larger forest-dwelling dung beetles (Scheffler 2005; Slade et al. 2011). The largest species recorded in our study, *Geotrupes opacus*, was found more frequently and at higher abundance in non-bison sites, while the increase in abundance in bison sites was due to two smaller *Onthophagus* species, *O. hecate* and *O. knausi*. Compensation by increasing small species would change both composition and abundance, but not necessarily total biomass, as we show here. Future work should determine if bison reintroduction consistently shifts community-weighted mean biomass of beetles by favoring smaller-bodied species, or smaller-bodied individuals within species. Notably, the smallest Scarabaeinae at our sites, *Onthophagus knausi*, was fairly

common in all bison sites but largely absent from non-bison sites.

Dung decomposition was also influenced by restoration age and bison presence, and increased decomposition may have been weakly related to the increases in beetle abundance that resulted from bison and site age. Dung mass loss was greater in the presence of bison, but this effect was most apparent in old restorations, less apparent in young restorations, and essentially absent in remnants. This seems to have been driven by lower dung mass loss in the old, non-bison site, which also had the lowest total abundance of the sites used in the decomposition experiment. It is possible that, as restorations age, they become less suitable habitat for dung beetles unless ungulates are present. Although abiotic conditions may have differed among sites, perhaps due to variation in vegetation structure, control pats within cages that excluded invertebrates consistently lost less mass, indicating that arthropods contributed to the decomposition. Decomposition was weakly correlated with beetle abundance, but not total beetle biomass or species richness, as has been observed in forest ecosystems (Horgan 2005; Slade et al. 2011). There may be insufficient variation in richness among our sites to detect a diversity effect on dung removal, with 13 of 15 sites having either two or three species. Large dung beetle species can increase total community biomass, as they may be one to two orders of magnitude greater in mass than the smallest species and can make larger contributions to dung removal (Larsen et al. 2005; Slade et al. 2011), driving total biomass–dung removal correlations. However, in our study the increased abundance of the two most common species (*O. hecate* and *O. knausi*), which are both quite small, may have been large enough in magnitude to overcome the limited volume of dung each individual beetle removes. Other coprophagous arthropods, including dung-dwelling flies and worms, likely contributed to mass loss as well, although they are generally considered less important (Rosenlew and Roslin 2008) and the presence of dung beetles, as well as fire (Scasta et al. 2015), reduces fly abundance and emergence from pats (Nichols et al. 2008).

Linking compositional differences in dung beetle communities to differences among sites in dung decomposition rates will require a closer examination of the morphological and functional characteristics of beetles in each community (Nichols et al. 2013; Audino et al. 2014). Such research should include a response–effect trait approach (Lavorel and Garnier 2002; Suding et al. 2008). This would allow identification of the “response traits” that mediate species responses to environmental drivers resulting from habitat management, and the “effect traits” that determine how much each species contributes to decomposition services. Information about response–effect functional traits would give managers more power to predict how decomposition may be influenced by environmental changes or shifts in management regimes that also alter beetle community structure. Further, it may allow better prediction of the impacts of nonnative dung beetles, which have been widely introduced in North America and elsewhere, and in many cases continue to expand their ranges (Kaufman and Wood 2012; Rounds and Floate 2012; Kadiri et al. 2014).

Throughout this study, we have interpreted dung beetle community changes as a result of bison reintroduction. It is

possible that these effects are not unique to bison and would result from the introduction of other large grazing mammals, especially if dung addition is the primary mechanism through which beetles are impacted. Dung beetle abundances and community composition respond to the presence of domestic cattle in other habitats (Lumaret et al. 1992; Verdú et al. 2007), and a study comparing beetles' preferences for bison and cattle dung found no differences (Tiberg and Floate 2011). However, bison also exhibit behavioral differences from cattle including differences in diet selection and wallowing behavior (Knapp et al. 1999). Our study does not allow us to compare bison impacts to cattle or other large grazing mammals because they are not present at the site. Detailed beetle sampling in regions where both bison and cattle, or other large grazers such as sheep (Jay-Robert et al. 2008), forage in comparable sites would be necessary to determine if the effects we document here are truly unique to bison or if other grazers could replicate these positive impacts.

Our study is significant because we show impacts of bison reintroduction on dung beetles and the decomposition of the bison's own dung. Bison reintroduction projects are occurring throughout their historical range, frequently on restored prairies, and we found that dung beetle communities respond quickly to bison reintroduction (here, less than 2 y). While an increase in dung beetles following the sudden availability of lots of dung may not be a particularly surprising result, the rapidity with which this occurred is encouraging evidence that restoration managers can reimpose ecosystem-level processes that support biodiversity of plants and other organisms, even in a reserve like Nachusa that is isolated from other extensive prairie habitat. An important additional step would be to compare these effects with domestic herbivores such as cattle or sheep, which also are used as management tools in grasslands. Tiberg and Floate (2011) showed that dung beetles generally preferred cattle dung over bison dung, so the bison effects we document here might even be amplified with cattle. If beetles respond similarly to domestic grazers, it could strengthen arguments for judicious use of cattle or sheep in situations where bison reintroduction is not feasible (Helzer et al. 2005).

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LITERATURE CITED

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